A LOWER CARBONIFEROUS BRACHIOPOD FAUNA FROM THE MANIFOLD VALLEY, STAFFORDSHIRE

by C. H. C. BRUNTON *and* C. CHAMPION

ABSTRACT. A silicified brachiopod fauna from North Staffordshire is described and thought to be early Viséan. It includes the new taxa *Lambdarina manifoldensis* and *Crurithyris nastus*, and other species showing North American Mississippian affinities. The fauna may indicate a relatively shallow-water environment with a low rate of sedimentation.

DURING the course of many years of collecting in the Staffordshire/Derbyshire border area one of us (C. C.) discovered the fauna here described in silicified limestones which crop out in the Manifold Valley, close to the village of Wetton (text-fig. 1). The fauna contained several species of unusual aspect as well as a totally new form and the material was sent to C. H. C. B. for comment. The distinctive new species proved to be most closely related to *Cardiarina*, an Upper Carboniferous genus known only from North America, but differs sufficiently to be separated as a new genus, here called *Lambdarina*, a name proposed in unpublished work by Dr. P. G. Morris for congeneric specimens he collected a few miles to the south of our localities at Waterhouses, on the Hamps river. (See addendum, p. 840.) The significance of this new species in British Lower Carboniferous rocks and the relationships of some of the other species, including the recognition of stenoscismataceans, add to the importance of this fauna.

Classification and nomenclature are, unless otherwise stated, as in the Treatise volumes (1965). The figured specimens are all housed in the British Museum (Natural History).

GEOLOGICAL SETTING

Bedded limestones, with variable dips, overlaid by obscurely bedded 'reefal' limestones are exposed on the south-west slope of Wetton Hill, above Leek Road, where it descends to the Manifold river, one-half mile west of Wetton village. Weathering of the lower group has revealed the presence, at certain levels, of well-preserved silicified fossils. These fossils are seen to have restricted vertical ranges, not being found in the 'reefal' limestones and only rarely 30 m or more below the 'reefal' limestones, where chert and authigenic quartz are frequently found in small amounts.

The fossils described below were extracted from the silicified limestones at the localities on the map (text-fig. 1, table 1). Specimens from A1 were from loose fragments at locality A and those from localities B and C came from loose blocks close by the river. Unfortunately most of the specimens of the new species of *Crurithyris* and *Lambdarina* came from the loose blocks rather than the *in situ* Leek Road localities.

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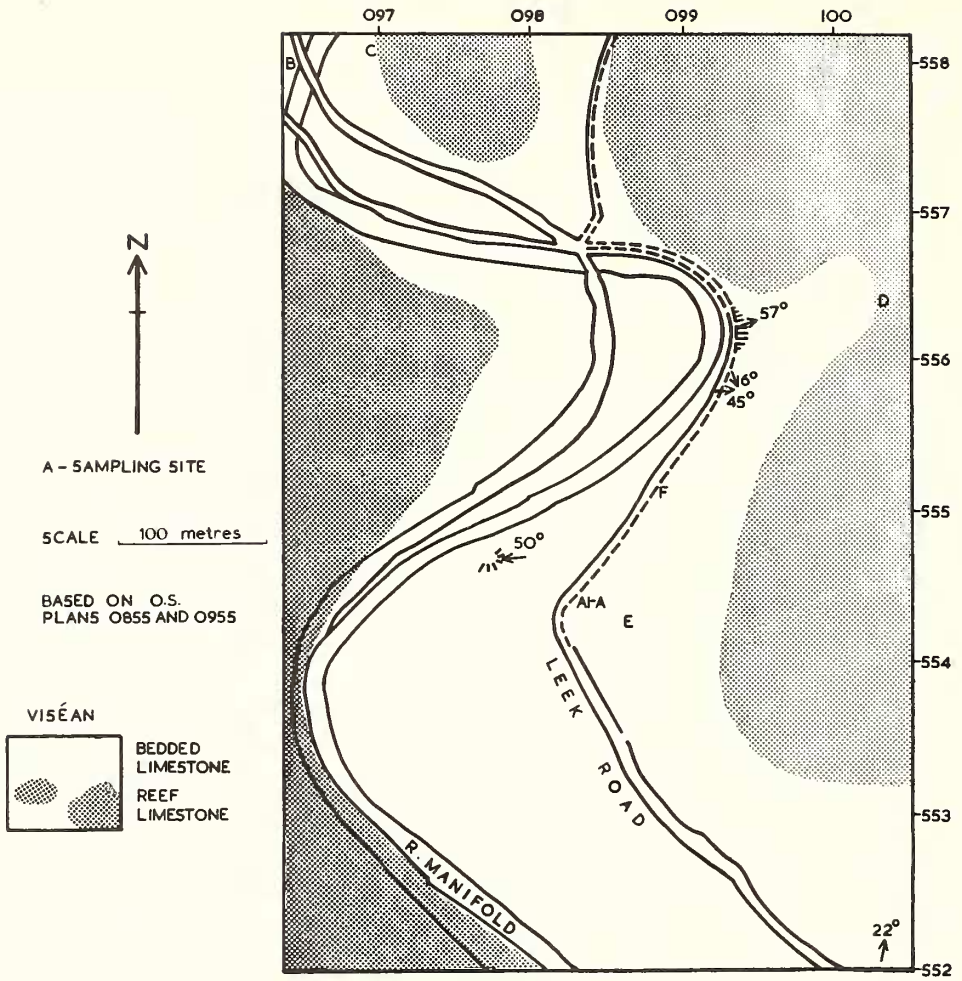

TEXT-FIG. 1. Geological sketch map of the area from which collections were made (marked A–F) approximately 1 km due west of Wetton village. Grid reference numbers, within the area SK, are given.

Partially silicified limestones occur widely in the Lower Carboniferous of Derbyshire and Staffordshire, but are not well documented. Thomas and Ford (1963) have described a silicified tabulate coral from Bradbourne, and Morris (1970) has noted silicified microfossils in the Hamps Valley, from where he has collected specimens of a new *Lambdarina* species and another related small brachiopod genus from rocks of high Tournaisian age.

The age of the bedded limestones from which the fauna was collected is in question. Prentice (1951) mapped the whole of Wetton Hill and this part of the Manifold Valley as, what Ludford (1951) and he called, the Waterhouses Limestone; he assigned this to the D Zone of the Viséan. However, Parkinson and Ludford (1964) believe that the Waterhouses Limestone, forming the east summit of Wetton Hill, is faulted

SPECIES \ LOCALITIES	A	A1	B	C	D	E	F
Acanthocrania cf laevis (Keyes)		2					
Schuchertella sp.	3						
Avonia (Quasiavonia) aculeata (J Sowerby)	1			2	?x		
'Stegacanthia' sp.		x			x		
Pleuropugnoides pleurodon (Phillips)						2	
Lambdarina manifoldensis sp.n.	1	15	72	ca.40			
Coledium seminulum (Phillips)	ca.40	23	ca.6	ca.7		1	3
Hustedia cf radialis (Phillips)	223	41	ca.25	15			
Hustedia ulothrix (de Koninck)	16	1		1		x	
Cleiothyridina fimbriata (Phillips)	ca.4	ca.5	ca.4	x			
Cleiothyridina deroissyi (Léveillé)	1	1					
Crurithyris nastus sp.n.	1	63	ca.200				3
Cyrtina cf burlingtonensis Rowley	1			1			
Fusella rhomboidea (Phillips)			x				
Spiriferellina perplicata (North)	ca.20	ca.20	ca.13	ca.3			
Girtyella saccula (J de C Sowerby)	5	5	x		?x		
Rhipidomella fragments	x				2		1

TABLE 1. The brachiopod fauna and localities from which the indicated numbers of specimens were collected. Samples from localities A1, B and C were not *in situ*, x indicates few fragments of the species; approximate numbers (*ca.*) are used for species in which complete specimens are augmented by some fragmentary material.

against C_2 or C_2S_1 limestones forming the west flank of the hill and extending into the Hamps and Manifold Valleys. Thus, according to Parkinson and Ludford, our silicified rocks are pre-D Zone in age and could perhaps be assigned to the Manifold Limestone-with-Shales. Prentice's 'conglomerate' (1951, p. 182) is topographically and stratigraphically below our collecting localities but does not crop out within the area of text-fig. 1. He interpreted this 'conglomerate' as separating rocks of C_1 age from those of D_1 age. Thin sections of this rock show that the limestone fragments are angular and in some instances fit one to another. The calcite matrix appears to have crystallized within the interspaces and to have assisted in splitting some of the limestone fragments, which are fossiliferous. We believe, therefore, that this rock represents a true 'reef' breccia derived from the near-by Thor's Cave 'reef' of C age and that, although it may represent a break, sedimentation of pre-D Zone age continued. Our view, therefore, is to favour Parkinson and Ludford's suggestion that these rocks are of C_2S_1 age and the brachiopods here described tend to support this in that *Lambdarina* is known from supposed C_1 limestones in Co. Dublin, Ireland, as well as the type area, but is unknown from D Zone rocks. *Crurithyris nastus* sp. nov. could be considered as ancestral to *C. urei* (Fleming), a species typical of the D Zone. In addition the small coral *Cladochonus*, especially *C. crassus* M'Coy is reported as common in C_2 and S Zone rocks (Thomas and Ford 1963; Parkinson and Ludford 1964). A species of *Cladochonus* like the young of *C. crassus* or *C. bacillarius* M'Coy is common in our collections.

THE FAUNA

Limestone samples were taken from several points west of Wetton village (text-fig. 1). After treatment in dilute hydrochloric or acetic acids the fauna was found to be composed predominantly of brachiopods together with abundant corallites of *Cladochonus*, a few gastropods, crinoid ossicles and plates, echinoid spines, and small bryozoan fragments. Silicification of the brachiopods was almost complete but replacement of the shell substance is by rather coarse silica, which in places has developed beekite rings. Some of the smaller specimens are silica-filled. Rarely small crystals of chalcopyrite impregnate the silica.

The fauna is enigmatical in that whilst it contains little of diagnostic stratigraphical importance (no microfossils have been found despite the use of acetic acid on some samples), it does yield some intriguing brachiopod species, e.g. the *Stegacanthia*-like species, the new *Lambdarina* species, the abundance of *Crurithyris nastus*, and the records of *Fusella* and *Cyrtina*, poorly known genera in our Lower Carboniferous rocks.

Thus age determination of these rocks remains equivocal. Some species, such as *Spiriferellina perplicata* and *Pleuropugnoides pleurodon*, are more typical of D strata. Most of the other species are wide ranging, whilst the two species compared with North American forms (viz. *Acanthocrania* cf. *laevis* and *Cyrtina* cf. *burlingtonensis*), as well as *Stegacanthia* s.s., are all commonly found in the Kinderhook and Osage, equivalent to the Tournaisian.

The brachiopod fauna is characterized by the preponderance of Spiriferida and by the small sizes of its constituent species, some of which are represented only by young specimens, e.g. the *Avonia* sp. and *Hustedia ulothrix*. The other species are commonly of small size, reaching less than 10 mm in length. The best preserved and most prolific species tend to have a highly biconvex profile and there is a high proportion of articulated shells of *Hustedia*, *Crurithyris*, *Lambdarina*, and *Coledium*. Almost all the larger *Spiriferellina* shells are disarticulated and, allowing for imperfections of silicification, external ornamentation is reasonably well preserved. Crushing of some shells occurred prior to silicification, particularly in *Hustedia* and to a lesser extent in *Crurithyris*. This crushing probably took place during sediment compaction and might have preferentially damaged larger specimens originally present in the fauna. However, silicified fragments of larger specimens are rare.

An incompletely silicified, and consequently fragmentary productacean has spines up to 30 mm long and it seems unlikely that this shell could have been moved any great distance after death. On the other hand, the general small size of the specimens and their biconvexity might suggest that they were winnowed from some near-by region.

With the exception of rare productaceans, which were passively sessile after the brephic stage, the other species were probably all attached to the substrate by pedicles. It seems unlikely that these species all had 'rooting' pedicles specialized for gripping in soft sediment and if not then there must have been sufficient firm substrate, either the bottom itself or skeletal debris, upon which their pedicles attached. If this were so a high rate of sedimentation is unlikely and it may well be that the area was one subject to slight current activity.

Ramsbottom (1970), in discussing British Namurian facies, and Samtleben (1971), in describing Bolivian Lower Permian brachiopods, suggest that *Crurithyris* indicates a near-shore or relatively shallow-water environment. In view of the 'reefal' deposits both below and above the rocks from which the fauna was collected and the conglomeratic breccia near by, a shallow-water environment seems likely. The small sizes of the individual species and apparent pedicle attachment of the brachiopods may support the view that they lived in conditions of shallow agitated water.

SYSTEMATIC DESCRIPTIONS

Class INARTICULATA Huxley 1869
Order ACROTRETIDA Kuhn 1949
Superfamily CRANIACEA Menke 1828
Genus ACANTHOCRANIA Williams 1943

Type species. Crania spiculata Rowley 1908, by original designation of Williams (1943, p. 71). Type specimen from the Louisiana Limestone, Missouri, U.S.A.

Acanthocrania cf. *laevis* (Keyes)

Plate 107, figs. 1–5

1894 *Crania laevis* Keyes, p. 40.
1914 *Crania laevis* Keyes; Weller, p. 47, pl. 1, fig. 33.
1968 *Acanthocrania* cf. *laevis* (Keyes); Brunton, p. 7, pl. 1, figs. 10–14.

Two specimens believed to be dorsal valves of *A. laevis* but differing in outline and profile come from locality A1. Silicification is not perfect so the external ornamentation is poorly preserved and the interiors are obscured by siliceous residues. Both specimens are small, being no more than 2 mm at their widest. One is 1·2 mm high (Pl. 107, fig. 1), the other only 0·6 mm high (Pl. 107, fig. 3). Although differing in shape the external ornamentation, where preserved, is identical and we believe the two to be conspecific. The external ornamentation can be seen to consist of radially arranged minute spines or papillae which tend to give the impression of a delicate radial ribbing. This ornamentation is characteristic of the genus.

The species *A. laevis* was fully described by Weller (1914) who first drew attention to the spinose exterior. It was first recorded and figured from Upper Palaeozoic rocks of Britain by Brunton (1968) in describing silicified specimens from the Viséan of Ireland. It is probably closely related to *A. spiculata* (Rowley), but without good type material with which to make comparison the two species must remain.

Class ARTICULATA Huxley 1869
Order STROPHOMENIDA Öpik 1934
Superfamily DAVIDSONIACEA King 1850
Family SCHUCHERTELLIDAE Williams 1953
Genus SCHUCHERTELLA Girty 1904

Three very small specimens of *Schuchertella*-like form have been collected from locality A; two are almost complete shells (Pl. 107, figs. 6–7) and one is an incomplete

dorsal valve (Pl. 107, figs. 8, 9). None is more than 3 mm wide. The unfigured specimen is broken at the umbo revealing neither dental plates nor a median septum. The cardinalia (Pl. 107, fig. 8) is *Schuchertella*-like in character and also similar to that of *Serratocrista* Brunton. What appears on the figure to be a median anterior node on the cardinal process is actually the broken edge of the valve floor. The external ornamentation is more like *Schuchertella* than *Serratocrista* so we suggest that the former genus was present in the fauna.

Superfamily PRODUCTACEA Gray 1840
Family OVERTONIIDAE Muir-Wood and Cooper 1960
Genus AVONIA (QUASIAVONIA) Brunton 1966

Type species. Productus aculeatus J. Sowerby 1814, p. 156, pl. 68, fig. 4.

Avonia (*Quasiavonia*) *aculeata* (J. Sowerby)

Plate 107, figs. 12–13

1814 *Productus aculeatus* J. Sowerby, p. 156, pl. 68, fig. 4.
1966 *Avonia* (*Quasiavonia*) *aculeata* (J. Sowerby); Brunton, p. 218, pl. 10, figs. 8–17; pl. 11, figs. 1–21.

Lectotype. Specimen from the Sowerby Collection, chosen by Muir-Wood (1951, p. 101) and housed in the British Museum (Nat. Hist.), B 60992.

This species was fully described, externally and internally, by Brunton (1966), using silicified material from Ireland. The Manifold silicified fauna has yielded a few young specimens of this species which reach almost 6·0 mm in length. Their rounded-quadrate to subcircular outline, lamellose ornament on the ventral valve, and suberect scattered spine bases are characteristics of this species. The spine bases of the juvenile clasping spines can be distinguished upon the ventral umbo, similar to those figured by Brunton (1966, pl. 11, fig. 9), but on none of the three complete specimens is a pedicle sheath preserved. The concave dorsal valve has an ornamentation of well-developed growth lines but appears to be devoid of spine bases. Normally the adults of this species have spinose dorsal valves, but the first-formed spines are either not preserved or did not grow until the valve was at least 5·0 mm long.

The species is rare, but has been collected from locality C (a loose block) and locality A, *in situ*.

EXPLANATION OF PLATE 107

Figs. 1–5. *Acanthocrania* cf. *laevis* (Keyes). 1–2, lateral and dorsal views of the more conical specimen. Locality A1. SEM × 25. BB 60241. 3–5, lateral and dorsal views (SEM × 25) and detail of external ornamentation (SEM × 160). Locality A1. BB 60240.

Figs. 6–9. *Schuchertella* sp. 6–7, dorsal and postero-dorsal views of a young shell from locality A. SEM × 23. BB 60242. 8–9, posterior and interior views of a young dorsal valve. SEM × 21. BB 60243.

Figs. 10–12. Cf. *Stegacanthia* sp. 10, incomplete dorsal valve interior from locality D, × 2. BB 60246. 11, general view of the ventral valve fragment from locality A1. The mid-line is marked by an arrow. × 1·7. BB 60245. 12, detail of mid-region of fig. 11 showing the line of large more erect spine bases. × 4·3.

Figs. 13–14. *Avonia* (*Quasiavonia*) *aculeata* (J. Sowerby). Dorsal and ventral views of the young specimen from locality A. × 5. BB 60244.


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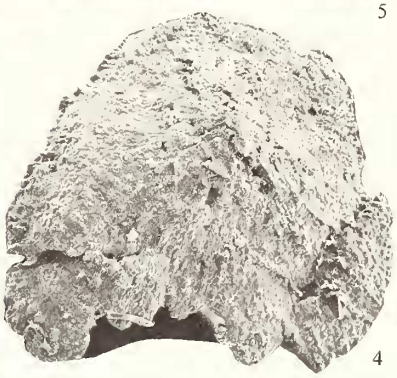
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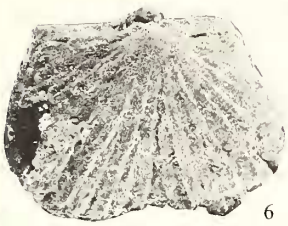
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BRUNTON and CHAMPION, Carboniferous brachiopods

Family ECHINOCONCHIDAE Stehli 1954
Genus STEGACANTHIA Muir-Wood and Cooper 1960

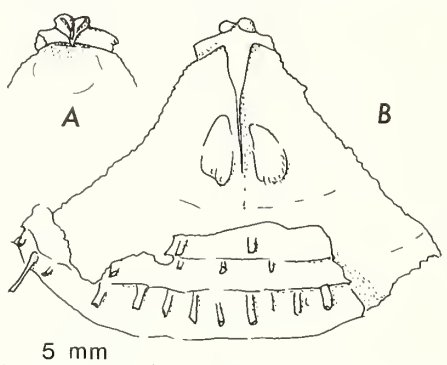
Type species. S. bowsheri Muir-Wood and Cooper 1960, p. 199, pl. 48, figs. 1–12, from the Lake Valley Formation, early Mississippian, Lake Valley, New Mexico, U.S.A.

Muir-Wood and Cooper (1960) and Muir-Wood (*in* Williams *et al.* 1965) placed this genus with the Overtoniidae but it would seem to us more closely allied to the genus *Pustula* and other genera placed within the Echinoconchidae.

cf. *Stegacanthia* sp. indet.

Plate 107, figs. 10–12

Fragments of a lamellose and highly spinose productacean have been recovered from limestone blocks at locality A1 and probably also from locality D. The external ornamentation of these fragments is of growth lamellae, which are well preserved peripherally, from which extend a single series of recumbent spines. Each spine is accompanied by a spine ridge posteriorly which may cause a fold in the anterior margin of the adjacent lamella (Pl. 107, fig. 12). This style of spinose ornamentation is very similar to that seen on *Stegacanthia* and were it not for the addition of one feature on our figured specimen it would certainly be placed within this genus. However, along the mid-line of the ventral valve there is a line of spine bases, one per lamina, which indicate that there was a line of rather larger suberect spines. This is not a feature of *Stegacanthia*, nor, so far as is known, a feature upon other highly spinose genera. Fragments of what would seem to be a second individual include a piece approximately 1 cm square which probably shows this same feature on two adjacent laminae. If there were, indeed, two specimens with a median line of suberect spines it is unlikely that the feature is a freak. The posterior regions of the valves are missing from locality A1, but the piece of shell from locality D includes the mid-region of the dorsal valve (Pl. 107, fig. 10). The sessile cardinal process supported by a wide but tapering low median septum and strong lateral ridges are characteristics seen also in the type species of *Stegacanthia*. Preservation of the valve exterior is poor, but from what can be seen it is almost certainly the same species as that from locality A1.



TEXT-FIG. 2. Camera-lucida sketch of the *Stegacanthia*-like specimen BB 60246. A, detail of the cardinal process exterior. B, internal view of the dorsal valve fragment with part of the ventral valve exterior preserved at the anterior margin. (See Pl. 107, fig. 10.)

In 1966, while commenting upon a few Irish silicified specimens he attributed to *Pustula* cf. *pyxidiformis* (de Koninck), Brunton indicated several similarities between his material and *Stegacanthia*. However, a restudy of the Irish material shows no sign of the median row of suberect spines and it cannot be considered as conspecific with our Manifold specimens.

Until more material of this species is available we can say no more than that this is probably a new species closely allied to *Stegacanthia bowsheri*. At a width estimated at about 50 mm, this was the largest species within the fauna.

Order RHYNCHONELLIDA Kuhn 1949
Superfamily RHYNCHONELLACEA Gray 1848
Family WELLERELLIDAE Likharev *in* Rzhonsnitskaya 1956
Genus PLEUROPUGNOIDES Ferguson 1966

Type species. Terebratula pleurodon Phillips 1836, p. 222, pl. 12, figs. 25–28. Ferguson (1966) first described this genus from type and other material in the British Museum (Nat. Hist.) and compared the type species with his new species *P. greenleightonensis*. He included within his new genus the species *Terebratula flexistria* Phillips and *T. proava* Phillips.

Pleuropugnoides pleurodon (Phillips)

Plate 108, figs. 1–4

1836 *Terebratula pleurodon* Phillips, p. 222, pl. 12, figs. 25–28.
1861 *Rhynchonella pleurodon* (Phillips); Davidson, p. 101 (*pars*), pl. 23, figs. 1–6.
1966 *Pleuropugnoides pleurodon* (Phillips); Ferguson, p. 355, pl. 23, figs. 1–6.

Type specimen. Lectotype chosen by Ferguson (1966), specimen illustrated by Phillips (1836), pl. 12, figs. 25, 26. Gilbertson Collection, British Museum (Nat. Hist.), B 361.

Diagnosis. Adults transversely elliptical rhynchonelliform shape, deep bodied with strongly uniplicate anterior commissure. Entirely costate, commonly with four ribs in the ventral sulcus. Dorsal median septum extending about one-third valve length, fused posteriorly to deep ventrally curved crura connected to short sockets by narrow outer hinge plates.

Discussion. This species is represented in our Manifold collections by only two specimens from locality E. Both are young and the better-preserved individual (BB 60247) is illustrated here (Pl. 108, figs. 1–4). The outline, being almost circular, is atypical for adult shells. However, from studies of conspecific material in which various growth stages are represented it can be seen that our specimen is of normal shape for its stage of development. Internal details are lacking in our material and use has been made of Irish silicified specimens to describe the cardinalia.

Family CARDIARINIDAE Cooper 1956
Subfamily LAMBDARININAE new subfamily
Genus LAMBDARINA new genus

Type species. L. manifoldensis sp. n. from Lower Viséan strata about one-half mile (1 km) west of Wetton, north Staffordshire.

Diagnosis. Cardiarinidae lacking a parathyridium, ventral umbo elongate and strongly bilobed body, each lobe extending antero-laterally at approximately 45° from mid-line.

Discussion. At an early stage in the preparation of this paper we became aware of work by Dr. P. G. Morris which included the description of new brachiopods

congeneric with *L. manifoldensis* for which he intended the generic name *Lambdarina*. We gratefully acknowledge the opportunity of seeing his specimens and prepared script enabling us to compare his species from Brownend Quarry with *L. manifoldensis*. We retain the name *Lambdarina* both in recognition of Dr. Morris's work and because of its suitability in describing the outline of these species.

The classification of the Cardiarinidae has always been uncertain. We retain the family within the Rhynchonellacea as there is no sign of endopunctation in our material although endopunctate shells found with *Lambdarina* specimens retain this feature.

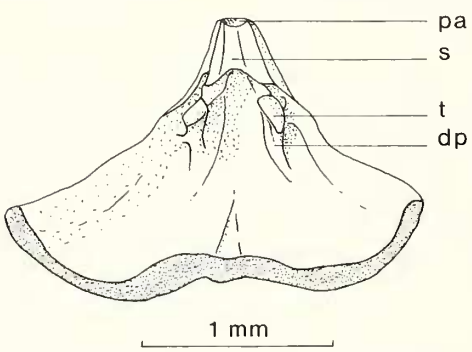
Lambdarina manifoldensis sp. nov.

Plate 108, figs. 5–11

Type specimens. From rocks believed to be of *c.* C_2S_1 age. Figured specimens, British Museum (Nat. Hist.), BB 60248 to BB 60252 and BB 60264, from locality B. Holotype, BB 60248.

Diagnosis. Lambdarina with rounded lobes about one-quarter of the shell's length, separated on ventral valve by low median ridge. Lateral profile plano-convex with ventral umbo slightly upcurved. Teeth and sockets well developed, low notothyrial platform posteriorly, and no differentiated crural processes.

Description. The largest of these small shells reaches 2·5 mm in length. The over-all lateral profile is plano to biconvex, the ventral valve umbo tending to curve dorsal of the commissural plane, but individually the lobes of both valves are strongly convex. External ornamentation is lacking, save for fine growth lines. The pedicle foramen is at the postero-dorsal extremity of the tube-like ventral valve umbo and the delthyrium is closed by a flat symphytium (Pl. 108, figs. 5, 11). The dorsal valve umbo is prominent medianly but somewhat flattened laterally. From a length of about 0·5 mm the dorsal valve is sulcate whereas in the corresponding position on the ventral valve there is a low ridge within the sulcus which divides the lobes of the shell (Pl. 108, fig. 6). The teeth are rounded in lateral profile and project above the valve margins (Pl. 108, fig. 11); they are narrow and extend antero-dorsally and slightly medianly to fit tightly behind the strong inner socket ridges of the dorsal valve. The teeth are supported by thin dental plates partially fused to the inner walls of the valve (text-fig. 3).



TEXT-FIG. 3. Postero-ventral view of the posterior portion of the ventral valve of *Lambdarina manifoldensis* sp. nov. showing the disposition of the teeth (t) and dental plates (dp), the symphytium (s), and pedicle aperture (pa). (See Pl. 108, fig. 11.)

Muscle scars have not been distinguished but the dorsal diductor muscle attachments were probably on the posterior ridge connecting the inner socket ridges and enclosing the notothyrial platform.

The species is named after the Manifold river.

Discussion. A different species of *Lambdarina* is known from Brownend Quarry, Waterhouses, about 3 miles south of our localities, as a result of the acid development of limestones near the Tournaisian/Viséan boundary by Dr. Morris, during his investigations of conodont faunas. This older species from Brownend Quarry is similar in shape and dimensions to *L. manifoldensis*, but differs in having relatively longer lobes and in lacking the low median ridge on the ventral valve of our species. From a brief study of Morris's material it can be seen that there are only slight internal differences; the inner socket ridges of *L. manifoldensis* are more strongly developed and do not recurve to the valve margins as appears to be the situation in Morris's specimens. Internally *L. manifoldensis* is similar to *Cardiarina cordata* Cooper, described from Pennsylvanian rocks of New Mexico, U.S.A. *Cardiarina* is furnished with a parathyridium (Cooper 1956, text-fig. 1) and it is this structure which most clearly differentiates the genus from *Lambdarina*. If there is a direct phylogenetic relationship between these two genera then it might be that the reduction of bilobation seen between the Brownend specimens and *L. manifoldensis* continued with the evolution of *C. cordata*. The development of the parathyridium might be associated with a reduction in the anterior growth of the inner socket ridges and teeth, both of which seem less well developed in the American species.

During early ontogeny, up to a length of from 0·8 mm to 1·0 mm, the outline of *L. manifoldensis* was triangular, the length being nearly twice the width (Pl. 108, fig. 7). Bilobation of the brachial cavity then developed but the mid-point of the anterior commissure continued to grow anteriorly, although less rapidly than the antero-lateral margins. Thus, once an individual had grown to about 1·6 mm long its relative shape, including the proportions of its lobes had reached that of the largest specimens collected, i.e. 2·5 mm long. The ventral umbo of juvenile specimens extended about 0·1 mm beyond the dorsal umbo and the pedicle aperture seems to have been connected to a small open delthyrium. During ontogeny the ventral umbo grew as a posteriorly tapering cone, on the dorsal side of which is a very narrow flat interarea and flat symphytium. The terminal aperture seems to have remained functional throughout life.

As yet this is the only published description of a species assigned to *Lambdarina*. However, in addition to the species from Brownend Quarry Dr. G. Sevastopulo of Trinity College, Dublin, has presented to the British Museum (Natural History) a few specimens (probably conspecific with the Brownend species) from uppermost Tournaisian shales of the Feltrim 'reef' in Co. Dublin, Ireland. No specimens that could be placed in the Cardiarinidae have been collected from the Viséan, D Zone, silicified faunas of Co. Fermanagh, Ireland, described by C. H. C. Brunton. Thus, as yet, our knowledge of the geological and geographical ranges of this and related species is very limited.

Habitat. Not having seen the relationship of any of these shells to the enclosing sediment it is impossible to do more than speculate upon the possible habitat of this species. In common with most other elements of the fauna the pedicle appears to have remained functional throughout life. In view of the small size of the species it seems likely that attachment was to a hard surface rather than by 'rooting' into relatively soft sediment. The morphology of the umbones and articulatory surfaces indicates

that the shell could not gape widely. It is likely, therefore, to have been able to adjust its position in free water using the pedicle, in contrast to non pediculate sessile and cemented species of brachiopod which tend to have wide gapes allowing the full exposure of the lophophore. In view of the small size of the specimens it might be that in life they attached to plants or animals and may have been epiplanktonic. Like the shells of *Cardiarina cordata* and the Brownend specimens, *L. manifoldensis* was attacked by boring organisms. In a sample of 54 specimens, 7 are bored of which only one is bored on the dorsal valve. All the holes are about 0·1 mm in diameter, positioned near the mid-line and within the mid one-third of the shell's length. There is some evidence for slight bevelling of the outer edges of the bored hole. The size corresponds to the minimum size of supposed gastropod borings on brachiopods described by Brunton (1966), but is less than that usually seen in shells and less than that expected from gastropod attack. If, as suggested above, *L. manifoldensis* was not sessile on a soft substrate it precludes the possibility of attack by burrowing organisms, such as the recent naticids, which approach their prey from below the sediment surface.

Superfamily STENOSCISMATACEA Oelert 1887 (1883)
Family STENOSCISMATIDAE Oelert 1887 (1883)
Genus COLEDIUM Grant 1965

Type species. Coledium erugatum Grant (1965, p. 96) from the Moorefield Formation (Upper Mississippian) of Oklahoma, U.S.A.

Stenoscismataceans, as such, are rarely recorded from British or European Lower Carboniferous rocks. However, utilizing specimens in the U.S. National Museum, Washington identified as *Terebratula globulina* Phillips and *T. rhomboidea* Phillips, Grant (1965) placed these British species within *Coledium*. Grant followed Davidson (1861) in placing *T. seminula* Phillips from the Lower Carboniferous of Bolland into synonymy with *T. globulina*, a Permian species originally described by illustration only. Inspection of the type material of *T. seminula* and specimens of *T. globulina* studied by Phillips, all housed in the British Museum (Nat. Hist.), leads to the conclusion that these species are distinctive. Despite the possibility of these three species names being used in British Upper Palaeozoic faunal lists, commonly linked with the generic names *Rhynchonella*, *Athyris*, or *Camarophoria*, records are few and this description is the first, with photographs, of a well-authenticated stenoscismatacean species from the British Lower Carboniferous.

EXPLANATION OF PLATE 108

Figs. 1–4. *Pleuropugnoides pleurodon* (Phillips). Dorsal, ventral, anterior, and lateral views of a specimen from locality E. × 3. BB 60247.

Figs. 5–11. *Lambdarina manifoldensis* gen. et sp. nov., from locality B. 5, dorsal view of an adult shell showing the symphytium. SEM × 22. BB 60248. 6, ventral view of an adult shell showing the low median ridge. Incomplete silicification replicates the growth lines externally and some of the fibrous shell postero-laterally. SEM × 20. BB 60264. 7, dorsal view of a young shell. SEM × 40. BB 60249. 8, oblique view of an incomplete young shell showing the teeth. SEM × 30. BB 60250. 9–10, oblique (SEM × 85) and posterior (SEM × 100) views of a dorsal valve showing the sockets (that on the right is filled with a broken-off tooth), and postero-median knob-like cardinal process. BB 60252. 11, postero-lateral view of an adult ventral valve showing the symphytium and strong teeth. (See also text-fig. 3.) SEM × 43. BB 60251.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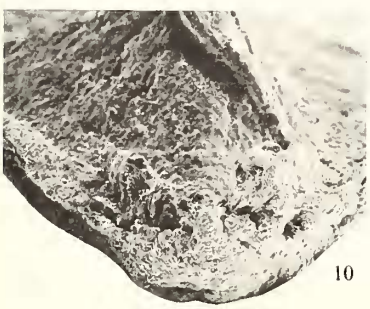
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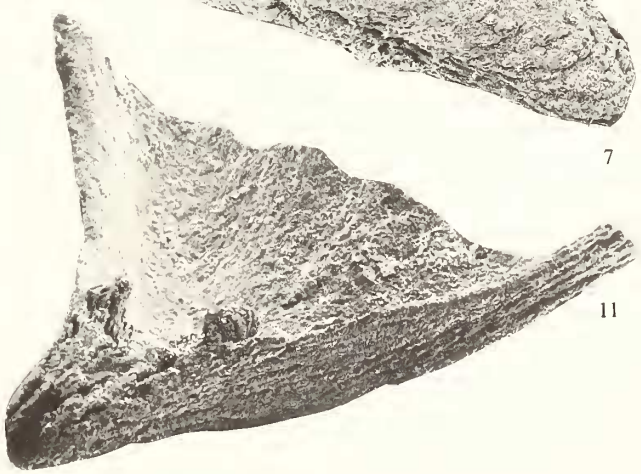
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BRUNTON and CHAMPION, Carboniferous brachiopods

Coledium seminulum (Phillips)

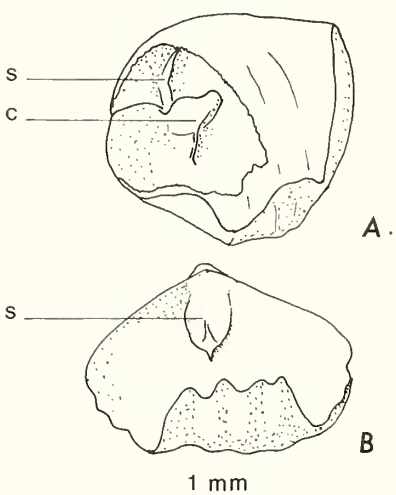
Plate 109, figs. 1–9

1836 *Terebratula seminula* Phillips, p. 222, pl. 12, figs. 21–23.
1861 *Camarophoria globulina* (Phillips); Davidson, p. 115, pl. 24, figs. 13–16.

Type specimen. T. seminula Phillips 1836, pl. 12, fig. 23, from Bolland, Yorkshire. Gilbertson Collection, British Museum (Nat. Hist.), B 355. Here selected as lectotype.

Diagnosis. Small (about 5 mm long) *Coledium*, slightly wider than long. Uniplicate anterior commissure modified normally by three ribs on dorsal fold with origins about 3·0 mm from dorsal umbo. Spondylium sessile posteriorly and elevated on low median septum anteriorly. Camarophorium narrow, concave postero-ventrally, vertically disposed anteriorly and supported by high median septum which does not extend anteriorly on valve floor.

Discussion. The complete specimen figured (Pl. 109, figs. 1–4) is slightly larger than the lectotype (which measures 4·2 mm long and 4·5 mm wide) and consequently has more fully developed lateral ribs, but in other external details the two appear to be identical. Unfortunately the interiors of type or topotypic material are unknown, but there seems little doubt that the present specimens should be assigned to *C. seminulum*. Davidson (1861) considered this species to represent the young of *C. rhomboidea* (Phillips) but inspection of the type material and sections of a specimen believed to be *rhomboidea* shows that these two species are distinctive both externally and internally; *C. rhomboidea* (Phillips) has a spondylium supported along its length by a well-developed median septum whilst that of *C. seminulum* is sessile save for its anterior end.



TEXT-FIG. 4. Drawings of an incomplete shell viewed postero-laterally (A) and of a ventral valve interior (B) of *Coledium seminulum* (Phillips) showing the spondylium (s) and camarophorium (c). Specimen A is illustrated in Plate 109, fig. 9.

This species is relatively common at the main collecting sites (table 1) and the complete collection contains about sixty-five more or less whole specimens; few, however, show the internal structures. Within the dorsal valve the camarophorium extends antero-ventrally as a trough-like process facing directly into the cavity of the spondylium (Pl. 109, fig. 9). The sockets and hinge plates appear to be short and give rise to small diverging and antero-ventrally directed crura. An intercamarophorial plate, as described by Grant (1965, p. 99) for the type species of *Coledium*, has not been observed in our material.

Being relatively common and represented by specimens of various sizes, it is possible to say a little about the ontogeny of this species. Shells down to a size of about 2 mm in length can be assigned to the species with some degree of certainty but there are many other individuals down to a length of about 1 mm for which a specific determination is doubtful. From the Manifold material it seems that the shell of *C. semi-*

nulum grew in a regular, smooth subcircular to broadly ovate form, with neither folding nor ribbing, up to a length of 3·0 mm to 3·5 mm. Beyond this length the rounded ribs and plication of the commissure began to develop; normally it is the ribs within the fold and sulcus region which developed first. During this growth period, and to maturity, shell accretion at the anterior commissure became increasingly opposed so as to increase considerably the depth of the shell cavity. Clearly, it was during this period too that the camarophorium changed its direction of growth from essentially anterior to ventral. Thus, the normal ontogenetic situation seems to have been that these shells were gently biconvex, narrow-bodied brachiopods up to a length of about 3·5 mm after which opposed growth at the anterior margins led to an increase in shell thickness (depth of body cavity) and a slight relative increase in shell width.

Grant (1965) pointed out that late Devonian and early Mississippian species of *Coledium* have an open pedicle foramen, which presumably remained functional during life. This condition would appear to have been true for *C. seminulum* and it is assumed that during life these shells were attached to the substrate by their pedicles. All the pedicle apertures are small (about 0·1 mm in diameter) and show no sign of abrasion at their margins. It is possible, therefore, that attachment was to a relatively soft substrate and/or that the habitat was one of quiet conditions.

Many of the specimens are sufficiently finely silicified for the fibrous nature of the secondary shell to be replicated and distinguishable at magnifications as low as × 10. At this magnification the shell fibres of the unsilicified type specimen can be seen. These fibres are distinctly larger than those of endopunctate species, such as *Hustedia* and *Spiriferellina* species, and slightly larger than those commonly seen in impunctate spire-bearing brachiopods.

Order SPIRIFERIDA Waagen 1883
Superfamily RETZIACEA Waagen 1883
Family RETZIIDAE Waagen 1883
Genus HUSTEDIA Hall and Clarke 1893

Type species. Terebratula mormoni Marcou 1858, p. 57, pl. 6, fig. 11, from near Salt Lake City, Utah, U.S.A. Type specimen not in Marcou Collection at British Museum (Nat. Hist.).

Hustedia cf. *radialis* (Phillips)

Plate 109, figs. 10–18

1836 *Terebratula radialis* Phillips, p. 223, pl. 12, figs. 40, 41.
1861 *Retzia radialis* (Phillips); Davidson, p. 87, pl. 17, figs. 19–21.
1887 *Retzia multicostata* de Koninck, p. 95, pl. 22, figs. 20–24.

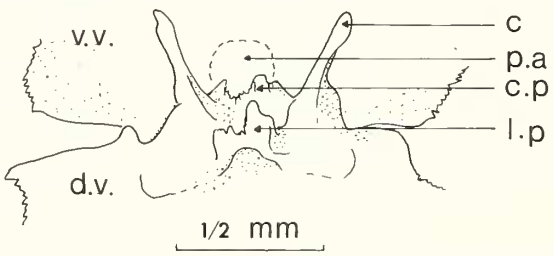
Type specimen. The specimen figured by Phillips (1836, pl. 12, figs. 40–41) from Bolland, Yorkshire. Gilbertson Collection, British Museum (Nat. Hist.), B 328.

Diagnosis. Small subcircular to broadly ovate *Hustedia* with slight dorsal sulcation and emarginate anteriorly. Entirely costate, dorsal valve with 15 to 17 rounded ribs.

Discussion. This species is one of the most prolific within the faunas collected from the area. Despite this we are unable to assign the name *radialis* with certainty because of

the confused situation still surrounding the specimens called *radialis* within the Gilbertson Collection used by Phillips for his 1836 publication. His collection includes specimens closely comparable to our material as well as specimens much larger (9·6 mm long), one of which should be considered as the type specimen on the grounds that it is probably the specimen figured by Phillips in 1836. Thus, there is some doubt as to whether both the large and small specimens should be called *radialis*. There are differences in the normal numbers of ribs on the dorsal valves of the type specimens and those from the Manifold Valley (19 to 21 and 15 to 17 respectively), but details of internal characteristics are unknown for the Gilbertson specimens. For the present, therefore, we compare our common *Hustedia* species to *radialis*, but recognize that it may prove to be distinctive. Recommendations upon the problem of *H. radialis* s.s. and a description of the species are beyond the scope of this paper but are being worked upon for publication elsewhere.

In Lower Carboniferous, Mississippian rocks of North America *Hustedia pygmaea* Rowley and *H. texana* Girty would appear to be similar to our species. Rowley (1900) described his species from 'the soft white cherts of the Lower Burlington limestone' of Missouri. It is a strongly biconvex species reaching about 6·5 mm in length and



TEXT-FIG. 5. The internal umbonal region of a young shell of *Hustedia* cf. *radialis* (Phillips) looking postero-ventrally and showing the cardinalia. The ventral valve (vv) is uppermost and the position of the pedicle aperture (pa) is indicated. The cardinal process (cp) and median ligulate process (lp) recurve postero-ventrally, but are incompletely preserved. The crura (c) diverge antero-ventrally.

EXPLANATION OF PLATE 109

Figs. 1–9. *Coledium seminulum* (Phillips). 1–4, dorsal, ventral, anterior, and lateral views of a specimen from locality B. ×4. BB 60253. 5–8, dorsal, ventral, anterior, and lateral views of a specimen from locality A. (Note the prominent halt in shell deposition at about three-quarters of the specimen length.) ×5. BB 60255. 9, oblique view into a broken shell from locality C showing the high camarophorium. (See also text-fig. 4.) ×7. BB 60254.

Figs. 10–18. *Hustedia* cf. *radialis* (Phillips). 10–12, dorsal, ventral, and lateral views of one of the larger specimens from locality A. ×7. BB 60256. 13–15, dorsal, ventral, and lateral views of a specimen from locality C. ×6. BB 60257. 16–18, lateral, dorsal, and ventral views of a young shell from locality C. ×10. BB 60258.

Figs. 19–21. *Hustedia ulothrix* (de Koninck). Lateral, dorsal, and ventral views of a young shell from locality C. ×7. BB 60259.

Figs. 22–23. *Cleiothyridina fimbriata* (Phillips). Ventral view of a young slightly crushed shell from locality A (×6), and detail of the external ornamentation antero-laterally (×22). BB 60260.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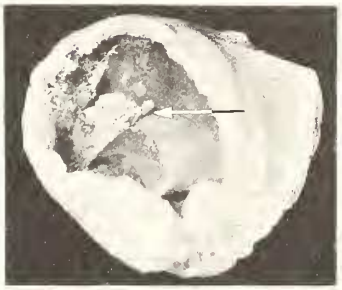
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differs from our specimens in lacking a dorsal valve sulcus and in having about 15 ribs on that valve. *H. texana* Girty (1926) is similar to the Manifold specimens in having a dorsal sulcus and occasionally an emarginate anterior commissure, but with about 19 ribs on the dorsal valve it is slightly more finely ribbed. *H. texana* appears to reach about 7 mm long but Girty's types are barely 5 mm long. Carter (1967) has redescribed this species and presents serial sections showing the internal structures. From these, and his plate figures, it seems that this mid Tournaisian species in the U.S.A. is closely related to the small forms called *H. radialis* and *H. multicostata* (de Koninck) in Britain and western Europe.

Most of the Manifold specimens are complete, silica-filled or slightly crushed so internal features are rarely seen. However, sufficient material is available to show the typical *Hustedia* cardinalia with its posteriorly recurved cardinal process extending into the ventral valve and the antero-ventrally projecting crural processes (text-fig. 5). The brachidium consists of laterally directed spiralia, each having at least three coils.

Hustedia ulothrix (de Koninck)

Plate 109, figs. 19–21

1843 *Terebratula ulotrix* de Koninck, pl. 19, fig. 5 (plate explanation only).
1861 *Retzia ulotrix* (de Koninck); Davidson, p. 88, pl. 18, figs. 14, 15.
1887 *Retzia ulothrix* (de Koninck); de Koninck, p. 92, pl. 22, figs. 1–4.

Type specimen. That figured by de Koninck in 1887 (pl. 22, figs. 1–4) from Tournai, Belgium, housed in the Brussels Museum. This specimen is accepted as type although it cannot be proved to be the specimen figured in 1843. The label with this specimen, in de Koninck's handwriting, uses the spelling *ulothrix*, as do his publications after 1843, and this spelling is here followed in the belief that *ulotrix*, used only on a plate explanation, was a printer's error.

Diagnosis. Hustedia with few (7 to 9 costae on dorsal valve) strong ribs and with width commonly exceeding length. Cardinal process lacking median ligulate process.

Discussion. The species is less common than *H. radialis*, accounting for only about 16% of all the *Hustedia* specimens. This order of abundance is seen elsewhere in localities from which full faunas have been collected by acid extraction. In museum collections *H. ulothrix* is normally over-represented as it is a much more obvious species to collect by traditional methods than is *H. radialis*.

The Manifold specimens do not attain the size of the type specimens or those figured by Davidson (1861, pl. 18; 1863, pl. 54), collected from near Wetton from rocks probably of D_1 age.

Superfamily ATHYRIDACEA M'Coy 1844
Family ATHYRIDIDAE M'Coy 1844
Subfamily ATHYRIDINAE M'Coy 1844
Genus CLEIOTHYRIDINA Buckman 1906

1850 *Cleiothyris* King, p. 137.

Type species. Atrypa pectinifera J. de C. Sowerby 1840, by original designation of King 1850.

An application to the International Commission on Zoological Nomenclature by

Brunton (1972) seeks the validation of *A. pectinifera* as type species of *Cleiothyridina*. This is on the grounds that Buckman's generic name was a substitute for *Cleiothyris* King, for which King had designated as type *A. pectinifera*. The type species of *Cleiothyridina* has commonly been quoted as *C. deroissyi* (Léveillé), but this designation was based upon a misconception of Léveillé's original description. *C. deroissyi* (Léveillé) (1835, pl. 2, figs. 18–20) is in reality a wider and more strongly folded species than *C. fimbriata* (Phillips), the species with which it has been confused for over one hundred years (Davidson 1861).

Cleiothyridina fimbriata (Phillips)

Plate 109, figs. 22, 23

1836 *Spirifera fimbriata* Phillips, p. 220 (no figure).
1861 *Athyris Royssii* L'Eveille; Davidson, p. 84 (pars), pl. 18, figs. 8–11 (fig. 11 from Phillips's original specimen).

Type specimen. From Viséan strata near Florence Court, Co. Fermanagh, Ireland. Phillips Collection, Oxford University Museum, E 1093.

The Manifold Valley material is assigned to this species with some doubt as it consists only of one young specimen (Pl. 109, fig. 22) and several very young specimens, a few millimetres long, together with fragments of larger specimens estimated to be 8 mm to 10 mm long. These larger fragments are ornamented by the spine-like frilly concentric outgrowths typical of *C. fimbriata*. It would appear, therefore, that this species was represented in the fauna by both adults and juveniles, possibly forming a breeding population.

Cleiothyridina deroissyi (Léveillé)

Plate 110, figs. 1–5

1835 *Spirifer De Roissyi* Léveillé, p. 39, pl. 2, figs. 18–20.
?1836 *Spirifera globularis* Phillips, p. 220, pl. 10, fig. 22.
1843 *Terebratula royssii* (Léveillé); de Koninck (*pars*), p. 300, pl. 21, fig. 1*a*?, *b–d*.
1887 *Athyris Roissyi* (Léveillé); de Koninck, p. 85, pl. 19, figs. 28, 29.
?1887 *Athyris squamigera* (de Koninck), p. 82, pl. 20, figs. 16–22.
?1914 *Cleiothyridina prouti* (Swallow); Weller, p. 474, pl. 79, figs. 13–16.

Type specimen. The original specimens of Léveillé are unknown, but probably came from the Tournai district.

Diagnosis. Outline subcircular when young to transversely elliptical when adult, strongly biconvex shell. Persistent fold and sulcus forming parasulcate anterior commissure. External ornamentation of closely spaced growth lines from which extend radially arranged finely spinose lamellae.

Discussion. A single complete young specimen was recovered from a block, not *in situ*, at locality A1. It measures 6·3 mm long, 6·5 mm wide, and 4·2 mm thick and the ventral sulcus starts at a length of about 3·5 mm. The sulcus, external ornamentation, and relatively greater thickness of this shell distinguish it from *C. fimbriata*. In *C. fimbriata* the lamellae are longer before splitting up into flat spatula-like spines, whilst the lamellae of *C. deroissyi* soon divide into needle-like spinose clusters.

Especially on young shells this needle-like ornamentation is radially arranged. Although these two species are readily distinguishable they have been confused since 1861 when Davidson figured *fimbriata* Phillips but placed it in synonymy with *deroissyi* Léveillé.

C. deroissyi is less common than *C. fimbriata* within the British Isles and probably also from Europe. *C. prouti*, from mid Tournaisian strata of the U.S.A., appears from the literature to be conspecific with *C. deroissyi* and to form a minor constituent of the North American fauna.

Superfamily CYRTIACEA Frederiks 1919/1924
Family AMBOCOELIIDAE George 1931
Genus CRURITHYRIS George 1931

Type species. Spirifer urei Fleming 1828, pl. 14, fig. 12. Lectotype selected by George (1931) from the Ure Collection, Hunterian Museum, Glasgow (L 1790), from high Viséan strata of Strathaven, Lanarkshire, Scotland.

Crurithyris nastus sp. nov.

Plate 110, figs. 6–16

Type specimens. Figured specimens are BB 60263 to BB 60268 (excluding BB 60264), from Viséan strata at locality B. In addition there are about 300 specimens from localities indicated on table 1.

Diagnosis. Crurithyris with longitudinally striated, tending to bifid, cardinal process. Inner socket ridges at about 45° to hinge line strongly fused to valve floor and differentiated from crural bases diverging from notothyrial platform. Ventral valve interior with low median ridge extending about three-quarters of the valve length.

Description. The shape and main internal features of these shells are figured (Pl. 110, figs. 11, 15 and text-fig. 6). The anterior commissure is rectimarginate to broadly and gently sulcate, the dorsal sulcus being slightly deeper than that on the ventral valve. Muscle scars are not clearly differentiated but the dorsal adductor scars are narrowly obovate in outline, raised on a low median ridge and extend anteriorly to about one-third of the valve's length (Pl. 110, fig. 11). The ventral muscle scars are separated

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EXPLANATION OF PLATE 110

Figs. 1–5. *Cleiothyridina deroissyi* (Léveillé). 1–3, dorsal, ventral, and lateral views of a small specimen from locality A. ×4. BB 60261. 4–5, dorsal and anterior views of a young shell showing some external ornamentation. Locality A1. ×3. BB 60262.

Figs. 6–16. *Crurithyris nastus* sp. nov., from locality B. 6–10, dorsal, ventral, lateral, anterior, and posterior views of a complete shell. ×5. BB 60263. 11, dorsal valve interior of a mature specimen showing the adductor muscle scars. SEM ×14. BB 60267. 12, ventral valve exterior. (See also text-fig. 6.) ×6. BB 60265. 13, ventral view of an incomplete shell showing part of the spiralia on the left side. ×5. BB 60266. 14, stereoscopic pair of the last specimen illustrating the crura (that on the right arrowed, A), part of the spiralia, the tooth ridges bordering the delthyrium internally (arrowed, B), and the articulation. ×10. BB 60266. 15–16, dorsal valve interior (SEM ×10) and detail of the cardinalia (SEM ×34). BB 60268.

Figs. 17–19. *Cyrtina* cf. *burlingtonensis* Rowley. Posterior, dorsal, and ventral views of the specimen from locality C. ×3. BB 60269.


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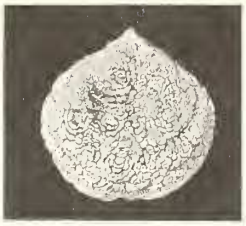
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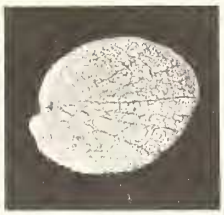
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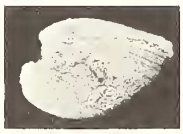
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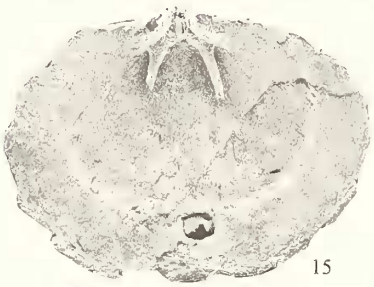
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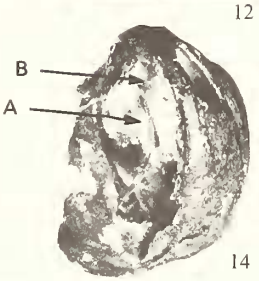

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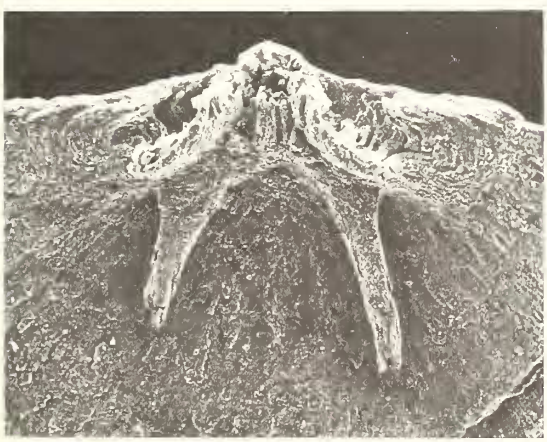
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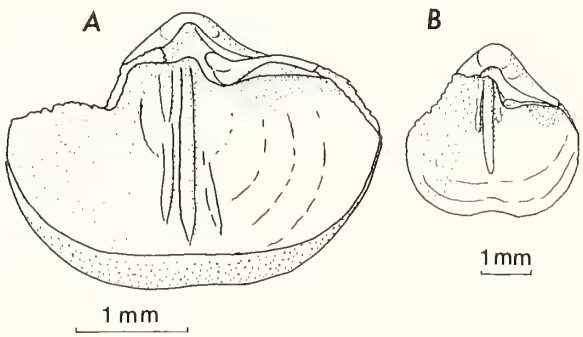
medianly by a low ridge; the pair of adductor scars are postero-medianly placed, surrounded by shell thickening posteriorly and are otherwise similar to the dorsal scars. The diductor scars are less well differentiated but appear to be widely spreading on the valve floor antero-laterally of the adductor scars.

The specific name is derived from *nastos* (Greek), meaning close-pressed or solid and refers to the characteristic socket ridges.

Discussion. The delicate spinose external ornamentation common to *Crurithyris* species was discussed by George (1931) who concluded, it is believed correctly, that the lack of this feature resulted from preservation failure. This ornamentation has not been seen on the present material and is thought to have been lost in the process of silicification. More delicately silicified specimens from elsewhere display the spinose ornamentation clearly. However, internal morphology is well replicated by the silica and enables a ready comparison to be made with similarly silicified *Crurithyris* specimens available from Ireland and attributed to *C. urei* (Fleming).



TEXT-FIG. 6. The ventral valve interior of *Crurithyris nastus* sp. nov. viewed postero-ventrally (A) and ventrally (B) showing the low median ridge and faint positions of the diductor muscle scars.

Externally *C. nastus* is similar to *C. urei*, the clearest difference being that the dorsal valve of *C. urei* is gently and regularly convex whilst that of the Manifold species is convex umbonally but becomes relatively flat anteriorly. Internally the differences are distinct. The cardinalia of *C. nastus* is illustrated (Pl. 110, fig. 16) and contrasts with that of *C. urei* in which the cardinal process is indistinct, the sockets are at a low angle from the hinge line (20°–25°) and terminate anteriorly free of the valve floor. The inner socket ridges of both species are strong, but those of *C. urei* are much more widely separated (105° as compared to *c.* 85° in *C. nastus*) and the crura extend anteriorly, subparallel to each other, directly from the socket bases and are free of the valve floor. In the Manifold specimens crural bases are differentiated from the inner socket ridges and diverge at about 60° from the base of the cardinal process; in older specimens they fuse to the valve floor posteriorly.

British Carboniferous *Crurithyris* species are most commonly recovered from D Zone limestones. *C. nastus* comes from rocks probably of basal Visean age and as such is intermediate in age between the younger species, such as *C. urei*, and the

Upper Devonian species *C. unguiculus* (J. de C. Sowerby). The morphology of the dorsal valve of our species is such that it could phylogenetically link *C. unguiculus* to *C. urei*. If this were so then we have evidence for a reduction in the development of crural bases and an increased separation of the anterior ends of the sockets from one another and from the floor of the valve. The cardinal process became less distinct, losing its bifid nature to become a tuberculate or ridged region between the apex of the inner socket ridges.

Rarely, in partially broken shells, the first coil of the laterally directed spiralia can be seen. This seems to be much the same as that of *C. urei* (as seen in Irish silicified specimens) and *C. planoconvexa* (Shumard), from the Permian of Bolivia, as illustrated by Samtleben (1972, pl. 8, fig. 3*a*, *b*). From about one-half of the dorsal valve length the lophophore support becomes a vertically disposed ribbon which twists ventro-laterally and then ventrally into the first coil. Evidence from other specimens indicates up to three full coils on each spiralia.

Superfamily SUESSIACEA Waagen 1883
Family CYRTINIDAE Frederiks 1912
Genus CYRTINA Davidson 1858

Type species. Calceola heteroclita Defrance 1828, p. 306.

Cyrtina cf. *burlingtonensis* Rowley

Plate 110, figs. 17–19; Plate 111, figs. 1–2

1893 *Cyrtina burlingtonensis* Rowley, p. 308, pl. 14, figs. 15–17.
1967 *Cyrtina burlingtonensis* Rowley; Carter, p. 354, pl. 34, figs. 1–8.
1968 *Cyrtina burlingtonensis* Rowley; Rodriguez and Gutschick, p. 1030, pl. 128, figs. 10–16.

The type species is not recorded by either Carter (1967), who presumes it to be in the University of Illinois collections, or Rodriguez and Gutschick (1968). However, these authors fully describe the specimens they ascribe to the species, the latter pair utilizing good silicified material from Montana, U.S.A. True *Cyrtina* species are poorly known from British Lower Carboniferous rocks, species such as *septosa* Phillips, *dorsata* M'Coy, and *carbonaria* M'Coy now being placed in the genus *Davidsonina* Schuchert and Le Vene 1929. A specimen figured by Davidson (1863, pl. 52, fig. 15) and called *Spiriferina insculpta* (Phillips) should be identified as a *Cyrtina*, possibly conspecific with the Manifold specimen. Within the British Museum (Nat. Hist.) collections there are a few specimens, believed to be conspecific, from Viséan rocks at Treak Cliff and Parkhouse Hill, Derbyshire, and from Wetton, Staffordshire. Brunton has a large collection of similar silicified specimens from Co. Fermanagh, Ireland, which are being described elsewhere.

Unfortunately the present study has yielded only one complete specimen, a poorly preserved dorsal valve and a few minute specimens possibly belonging to this species (Pl. 111, figs. 3–5). For this reason the specific designation must be in doubt. However, externally the complete specimen seems identical to those described by Carter or by Rodriguez and Gutschick. The specimen is 6·7 mm in over-all length, 8·0 mm wide, and 5·0 mm high, dimensions which fall very close to those given by Carter (1967, p. 357). Internal morphology is known only from the one incomplete dorsal

valve (Pl. 111, fig. 2). However, from what can be seen it is evident that the cardinalia resembles that illustrated by Rodriguez and Gutschick (1968). The inner socket ridges closely confine the triangular, highly sculptured and ventrally directed myophore face of the cardinal process. The crural bases are poorly differentiated from the inner socket ridges and are joined to the valve floor at the base of the cardinal process. There is a low, indistinct median ridge. This small *Cyrtina* species does seem to be rare in British (exclusive of Ireland) Lower Carboniferous rocks; even in regions of prolific brachiopods, collected over many years, the number of specimens recorded or seen in collections is small.

Superfamily SPIRIFERACEA King 1846
Family SPIRIFERIDAE King 1846
Genus FUSELLA M'Coy 1844

Type species. Spirifera fusiformis Phillips 1836, p. 210, pl. 9, figs. 10, 11, from Bolland, Yorkshire. Specimen in the Gilbertson Collection of the British Museum (Nat. Hist.), B 249.

Diagnosis. Small (up to approx. 30 mm wide), fusiform (transversely narrowly rhombic) spiriferides with sharply pointed cardinal extremities and finely denticulate high ventral interarea. Ventral sulcus bordered by a pair of prominent ribs plus seven to ten additional ribs. Dental plates short, subparallel and fused umbonally by shell thickening which fills delthyrial apex. Dorsal fold may be weak with indistinct median rib.

Discussion. The characteristics of this genus have been ill-defined owing to the rarity of the type species and the name has been used in the past for a variety of differing spiriferide forms. Conversely in recent years other genera have been described which are closely related to *Fusella*, such as *Amesopleura* Carter 1967 (? = *Voiseyella* Roberts 1964). The genus *Mirifusella* Carter 1971 is said to be 'most similar to *Fusella* M'Coy' (Carter 1971, p. 250). In fact the two differ considerably in their external morphology, *Mirifusella* tending to be longer than wide and having rounded cardinal extremities. A recent restudy of the type specimen plus silicified material from Ireland allows a more complete description of the genus and this is to be published elsewhere by C. H. C. B. The genus is represented in the present fauna by a single incomplete specimen, plus some fragments, believed to be *F. rhomboidea* (Phillips), a species closely related to *F. fusiformis* (Phillips).

EXPLANATION OF PLATE 111

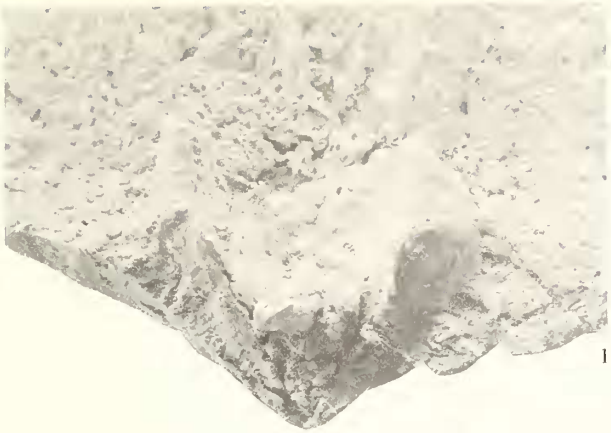
Figs. 1–2. *Cyrtina* cf. *burlingtonensis* Rowley. Detail of the dorsal cardinalia (SEM × 50) of an incompletely preserved valve (SEM × 15) from locality A. BB 60270.

Figs. 3–5. ?*Cyrtina* sp. Lateral, posterior (SEM × 30), and ventral (SEM × 20) views of a young shell from locality A1. BB 60279.

Figs. 6–7. *Fusella rhomboidea* (Phillips). Dorsal and ventral views of the incomplete shell from locality B. × 3. BB 60271.

Figs. 8–13. *Spiriferellina perplicata* (North). 8–9, exterior and interior of a ventral valve from locality C. × 3. BB 60274. 10–11, ventral and posterior views of a slightly crushed specimen from locality A. × 3. BB 60272. 12, dorsal view of an incomplete juvenile shell from locality B. × 3. BB 60275. 13, fragment of a dorsal valve interior showing the ridges bounding the adductor muscle scars. × 4. BB 60273.

Figs. 14–16. *Girtyella saccula* (J. de C. Sowerby). 14, dorsal view of a slightly crushed shell from locality A. × 3. BB 60278. 15–16, lateral and dorsal view of a specimen from locality A1. × 3. BB 60277.



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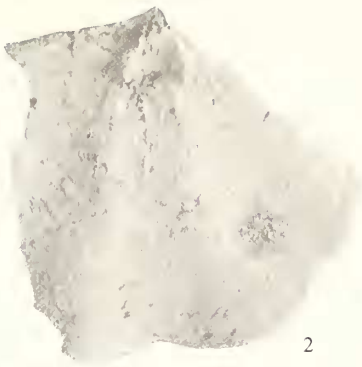

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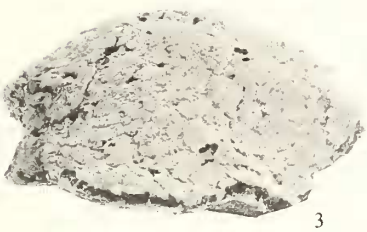

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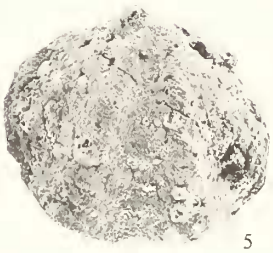

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BRUNTON and CHAMPION, Carboniferous brachiopods

Fusella rhomboidea (Phillips)

Plate 111, figs. 6–7

1836 *Spirifera rhomboidea* Phillips, p. 217, pl. 9, fig. 8.
1858 *Spirifera convoluta* var. *rhomboidea* Phillips; Davidson, p. 35, pl. 5, fig. 2.

Type specimen. Spirifera rhomboidea Phillips from Bolland, Yorkshire. Gilbertson Collection, British Museum (Nat. Hist.), B 236.

Diagnosis. Relatively large *Fusella* with prominent ribs, fold, and sulcus. Dorsal fold with low median rib and first pair of bordering ribs bifurcating close to umbo. Ventral interarea high and strongly curved, delthyrium narrow and teeth supported by short, narrowly divergent and vertically subparallel dental plates which converge slightly medianly.

Discussion. Details of the external ornamentation are lacking from the type specimen but can be seen on the silicified Manifold specimen to consist simply of variously developed growth-lines producing a slight imbrication. Otherwise the exterior is smooth. Incomplete silicification has resulted in the loss of most internal features on this specimen. All that can be seen is part of one dental plate and signs of the umbonal shell thickening.

Superfamily SPIRIFERINACEA Davidson 1884
Family SPIRIFERINIDAE Davidson 1884
Genus SPIRIFERELLINA Frederiks 1919 (1924)

Type species. Terebratulites cristatus von Schlotheim 1816, p. 28. Lectotype chosen by Campbell (1959, p. 350) and housed in the Geologisch-Paläontologisches Institut und Museum, Berlin.

Spiriferellina perplicata (North)

Plate 111, figs. 8–13

1920 *Spiriferina perplicata* North, p. 219, pl. 13, figs. 7*a–c*, 10.

Type specimen. That figured by North (1920) on plate 13 as fig. 7*a–c*, from D_1 Zone strata of Treak Cliff, Castleton, Derbyshire. J. W. Jackson Collection, Manchester Museum, L 11601. North (1920, p. 219) gives Peaks Hill as the locality but J. W. Jackson (1952) has pointed out that this is an error and that the true locality is Treak Cliff, as stated on the box containing the specimen.

Diagnosis. Transverse *Spiriferellina* with greatest width at hinge-line. Adult shells with six strongly developed ribs on each side of mid-line on ventral valve. Concentric lamellae most prominent on rib crests. Anterior edges of dental plates diverge slightly to valve floor. Ventral median septum high anteriorly and extending about one-half of length of shell. Cardinal process low, from base of which extends pair of ridges laterally bordering adductor scars.

Description. That given by North (1920, p. 219) adequately describes the exterior of this species. The only internal details that he gave indicated the presence of dental plates and a ventral median septum. The morphology of the interiors of both dorsal and ventral umbones are illustrated here (Pl. 111, figs. 9, 13).

Discussion. The type species of *Spiriferellina* was redescribed in 1959 by Campbell

and later Logan (1964) reviewed the history of the classification of *Spiriferina* d'Orbigny and concluded that *Spiriferellina* should include *S. insculpta* (Phillips), *S. octoplicata* (J. de C. Sowerby), and *S. perplicata* (North), all Carboniferous species believed to be closely related to the type species, *S. cristata*, of Permian age. Thus in the British Lower Carboniferous we have two endopunctate spiriferinide genera, *Spiriferellina* and *Punctospirifer* North, based upon the species *P. scabricosta* North; the latter being distinguished externally by its greater number of less angular and lower ribs and relatively wide rounded ventral sulcus.

Spiriferellina perplicata is most closely related to *S. insculpta* (Phillips), but the two differ in that the latter species is more strongly biconvex, owing to having a strongly convex dorsal valve, and the number of ribs on each side of the ventral mid-line of adult specimens is normally only four. On particularly well-preserved specimens of *S. insculpta* there is a fine spinose ornamentation, a feature which has not been observed on *S. perplicata*. Internally the two species are similar.

Order TEREBRATULIDA Waagen 1883
Superfamily DIELASMATACEA Schuchert 1913
Family DIELASMATIDAE Schuchert 1913
Genus GIRTYELLA Weller 1911

Type species. Harttina indianensis Girty 1908, p. 293, pl. 19, figs. 6–15. Pella beds, Pella, Iowa, U.S.A. Mississippian.

Weller first described his genus *Girtyella* in 1911 (p. 442), not in 1914 as stated by Muir-Wood (1951) and the Treatise (1965). It was separated from *Dielasma* on account of its inner hinge plates being supported on a median septum. These plates should be depressed medianly rather than forming a flat cardinal plate as shown in the Treatise (1965: H 754), and in some species it may be that the median septum is low so that the septalium is virtually sessile anteriorly. However, the inner hinge plates do not separate dorso-medianly to expose the valve floor, as in *Dielasma*.

Girtyella saccula (J. de C. Sowerby)

Plate 111, figs. 14–16

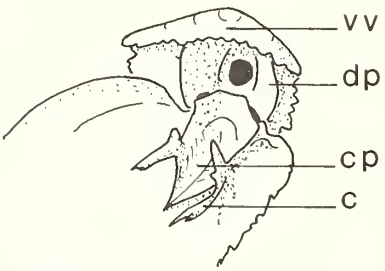
1824 *Terebratula sacculus* J. de C. Sowerby, p. 65, pl. 446, fig. 1.
1951 ?*Girtyella sacculus* (J. de C. Sowerby); Muir-Wood, p. 113, pl. 5, fig. 1*a–c*.

Type specimen. Lectotype selected by Muir-Wood (1951) from the Sowerby Collection, Lower Carboniferous of Derbyshire. British Museum (Nat. Hist.), B 61653.

Diagnosis. Small (up to about 15 mm long) strongly biconvex shell with emarginate anterior in adults resulting from opposite ligate to narrowly uniplicate folding. Commonly with marked growth lines anteriorly. Dorsally curved epithyridid ventral umbo.

Discussion. This species is rare within the Manifold faunas, being represented by about ten reasonably preserved specimens measuring up to 8 mm long. Two broken specimens show some of the internal structures and enable the assignment of this species to *Girtyella*. The ventral valve has well-developed dental plates and within the dorsal valve the crural or inner hinge plates are V-shaped and supported medianly on

a low median septum. Differentiation between this median region and the flanking outer hinge plates and the inner socket ridges is weak, but is indicated by a change in angle at the point from which the crura extend anteriorly (text-fig. 7). The extent of the crura and complete form of the loop have not been observed.



TEXT-FIG. 7. An oblique view of the dorsal valve interior plus umbonal region of the ventral valve, of *Girtyella saccula* (J. de C. Sowerby). The illustration is composite from two partly preserved specimens. Ventral valve (vv), dental plate (dp), crural plate (cp), and a broken portion of a crus (c).

The paucity of this species in the Manifold limestones is not surprising since normally it is found abundantly only in 'reefal' limestones. However, specimens assigned to the species are found widely and vary greatly in external form. The lectotype measures 16·3 mm long, 14·8 mm wide, and 10·8 mm thick. This compares closely with specimens of *G. indianensis* (Girty), the type species, and falls about midway within the range of sizes seen in museum collections, where specimens reach at least 30 mm long. Sowerby's figures (1824, pl. 446, fig. 1) illustrate the variation seen within specimens attributed to *G. saccula*; the top-left specimen (B 61654) being small (11 mm long) and ventrally sulcate from a point about 5 mm in front of the umbo. The central figure, the lectotype, is larger and specimens like this tend to develop a ventral sulcus only after a length of at least 10 mm, and the anterior commissure is less strongly folded than that of the small specimens. The top-right illustration is of a younger specimen (6·6 mm long) lacking any prominent sulcation. Specimens in museum collections, said to be from single localities, are indicative of continuous variation between these two forms, but whether we are dealing with intraspecific variation or not is beyond the scope of the present study. As there is no strongly developed ventral sulcus on the few specimens extracted from the Manifold limestones they are probably the young of the larger form of *G. saccula*.

ADDITIONAL MATERIAL

In addition to those specimens already described there are many minute individuals, less than 3 mm long, which are difficult to classify. Some are almost certainly the young of *Coledium* and are mentioned under that genus. Of the others from locality A (*in situ*) four specimens may be the young of *Cyrtina*; the silicified shell looks as if it may be a replacement for endopunctate shell, and the ventral valve is quite strongly convex in profile (Pl. 111, figs. 3–4). Other problematical small specimens appear to have been impunctate, they are ventribiconvex in profile, have a ventral median sulcus, and the narrow ventral interarea has an open delthyrium. The only adult species in the fauna with which these may be related is *Crurithyris nastus*.

Fragments of a *Rhipidomella* species occur at locality A. Otherwise this genus has been recovered from locality D, where it occurs with some minute indeterminate brachiopod specimens and fragments of the gastropod *Anomphalus*, and also at locality F.

REFERENCES

BRUNTON, C. H. C. 1966. Silicified productoids from the Viséan of County Fermanagh. *Bull. Br. Mus. nat. Hist.* (*Geol.*), **12**, 173–243, pls. 1–19.

—— 1968. Silicified brachiopods from the Viséan of County Fermanagh (11). Ibid. **16**, 1–70, pls. 1–9.

—— 1972. *Cleiothyridina* Buckman, 1906 (Brachiopoda): Proposed validation under the plenary powers. *Bull. Zool. Nomencl.* **29**, 142–144.

CAMPBELL, K. S. W. 1959. The type species of three Upper Palaeozoic punctate spiriferoids. *Palaeontology*, **1**, 251–363, pls. 58–60.

CARTER, J. L. 1967. Mississippian brachiopods from the Chappel Limestone of central Texas. *Bull. Amer. Paleont.* **53** (238), 253–488, pls. 13–45.

—— 1971. New early Mississippian silicificd brachiopods from Central Iowa. *Smithson. Contribn. Paleobiol.* **3**, 245–255, pls. 1–2.

COOPER, G. A. 1956. New Pennsylvanian brachiopods. *J. Paleont.* **30**, 521–530, pl. 61.

DAVIDSON, T. 1861–1863. British Carboniferous Brachiopoda. *Palaeontogr. Soc.* (*Monogr.*), **2**, (5), 81–280, pls. 17–60.

FERGUSON, J. 1966. Variation in two species of the Carboniferous brachiopod *Pleuropugnoides*. *Proc. Yorks. Geol. Soc.* **35**, 353–374, pl. 23.

GEORGE, T. N. 1931. *Ambocoelia* Hall and certain similar British Spiriferidae. *Quart. J. geol. Soc. Lond.* **87**, 30–61, pls. 3–5.

GIRTY, G. H. 1926. Mississippian formations of San Saba County, Texas, III. The macrofauna of the limestone of Boone age. *U.S. geol. Surv. Prof. Paper*, **146**, 24–43, pls. 5–6.

GRANT, R. E. 1965. The brachiopod superfamily Stenoscismatacea. *Smiths. Misc. Coll.* **148**, 1–192, pls. 1–24.

JACKSON, J. W. 1952. *Catalogue of type and figured specimens in the Geological Department of the Manchester Museum*. Mus. Publ. **6**, 170 pp. Manchester.

KONINCK, L. G. DE. 1843. *Descriptions des animaux fossiles*, pp. 241–480. Liege.

—— 1887. Faune du calcairc Carbonifère de la Belgique. Brachiopodes. *Annls Mus. r. Hist. nat. Belg.* **14** (6), i–ix, 1–154, pls. 1–37.

LÉVEILLÉ, C. 1835. Aperçu géologique de quelques localités très riches en coquilles sur les frontières de France et de Belgique. *Mem. Soc. géol. France*, **2**, 29–40, pl. 2.

LOGAN, A. 1964. An Indo-pacific spiriferinid from the Triassic of North-eastern British Columbia. *Bull. Canadian Petrol. geol.* **12**, 692–718, pls. 1, 2.

LUDFORD, A. 1951. The stratigraphy of the Carboniferous rocks of the Weaver Hills district, North Staffordshire. *Quart. J. geol. Soc. Lond.* **106**, 211–230, pl. 16.

MORRIS, P. G. 1970. Holothurian spicules from the Lower Carboniferous near Waterhouses, North Staffordshire. *Mercian Geol.* **3**, 353–359.

MUIR-WOOD, H. M. 1951. The Brachiopoda of Martin's 'Petrificata Derbiensia'. *Ann. Mag. nat. Hist.* **4**, 97–118, pls. 3–6.

—— and COOPER, G. A. 1960. Morphology, classification and life habits of the productoidea (Brachiopoda). *Mem. geol. Soc. Amer.* **81**, 1–447, pls. 1–135.

NORTH, F. J. 1920. On *Syringothyris* Winchell, and certain Carboniferous Brachiopoda referred to *Spiriferina* D'Orbigny. *Quart. J. geol. Soc. Lond.* **76**, 162–227, pls. 11–13.

PARKINSON, D. and LUDFORD, A. 1964. The Carboniferous Limestone of the Blore-with-Swinscoe district, northeast Staffordshire, with revisions to the stratigraphy of neighbouring areas. *Geol. J.* **4**, 167–176, pl. 8.

PHILLIPS, J. 1836. *Illustrations of the geology of Yorkshire. Part II. The Mountain Limestone District*. 253 pp., 25 pls. John Murray, London.

PRENTICE, J. E. 1951. The Carboniferous Limestone of the Manifold Valley region, North Staffordshire. *Quart. J. geol. Soc. Lond.* **106**, 171–209, pl. 15.

RAMSBOTTOM, W. H. C. 1970. Carboniferous faunas and palaeogeography of the South West of England region. *Proc. Ussher. Soc.* **2**, 144–157.

RODRIGUEZ, J. and GUTSCHICK, R. C. 1968. *Productina*, *Cyrtina*, and *Dielasma* (Brachiopoda), from the Lodgepole Limestone (Mississippian) of southwestern Montana. *J. Paleont.* **42**, 1027–1032, pl. 128.

ROWLEY, R. R. 1900. Descriptions of new species of fossils from the Devonian and subcarboniferous rocks of Missouri. *Amer. Geol.* **25,** 261–272, pl. 5.

SOWERBY, J. DE C. 1824. *The Mineral Conchology of Great Britain*, vol. 5, 63–138, pls. 444–485.

SAMTLEBEN, C. 1971. Zur kenntnis der produktiden und spiriferiden des Bolivianischen Unterperms. *Beih. geol. Jb.* **111,** 1–163, pls. 1–11.

—— 1972. Feinbau und wachstum von spiriferiden-armgerusten. *Palaont. Z.* **46,** 20–33, pls. 5–8.

THOMAS, H. D. and FORD, T. D. 1963. A new tabulate coral from the Viséan of Derbyshire. *Proc. Yorks. geol. Soc.* **34,** 45–50.

WELLER, S. 1911. Genera of Mississippian loop-bearing Brachiopoda. *J. Geol.* **14,** 439–448.

—— 1914. The Mississippian Brachiopoda of the Mississippi Valley Basin. *Illinois State geol. Surv. Mon.* **1,** 508 pp., 83 pls. Urbana.

WILLIAMS, A. 1965. *In* MOORE, R. C. (ed.). *Treatise on Invertebrate Paleontology. Pt. H, Brachiopoda*, 927 pp., 746 figs. Kansas.

WILLIAMS, J. S. 1943. Stratigraphy and fauna of the Louisiana Limestone of Missouri. *U.S. geol. Sur. Spec. Paper*, **203,** 1–131, pls. 1–9.

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ADDENDUM (added August 1974)

It has proved impossible to contact Dr. P. G. Morris for the purpose of discovering the reference to his paper describing *Lambdarina*. It seems likely that our paper will now be published before that of Dr. Morris, so in order to reduce taxonomic confusion we have emended our text at this late date to avoid referring to an unpublished paper. At the beginning of 1972 C. H. C. B. had arranged to discuss with Dr. Morris the relationships of our faunas and prospects of joint authorship. However, circumstances did not allow this meeting until January 1973 when C. H. C. B. saw Dr. Morris, his material and completed script awaiting submission for publication. At that time this paper was in the earliest stages of drafting and we continued in the belief we would be comparing our material to that already published by Dr. Morris. In retaining the name *Lambdarina*, which we anticipated as by now being published, we acknowledge Dr. Morris's recognition of these unusual brachiopods in the Waterhouses area.